Predicting Species Interactions Based on Behaviour: Predation and Competition in Container-Dwelling Mosquitoes

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Summary

1. We tested the hypothesis that competitive ability and vulnerability to predation are primarily products of behaviour using larvae of three container-dwelling mosquitoes.

2. *Aedes aegypti* was more active, spent more time browsing, more time at the bottom and less time resting than did *Aedes triseriatus*. These differences lead to the prediction that *A. aegypti* is a more effective forager and competitively superior to *A. triseriatus*.

3. In the presence of the predator *Toxorhynchites rutilus*, *A. aegypti* spent more time thrashing, less time resting, more time at the bottom and less time at the surface than did *A. triseriatus*. These differences lead to the prediction that *A. aegypti* is more vulnerable to predation than *A. triseriatus*.

4. Survival time with *T. rutilus* was significantly lower for *A. aegypti* than for *A. triseriatus*, confirming the prediction of greater short-term (minutes) vulnerability of *A. aegypti*.

5. When exposed to *T. rutilus* (hatch to adult), cohorts of *A. aegypti* usually failed to produce adults, but cohorts of *A. triseriatus* always produced adults. At high *Aedes* density, predation by *T. rutilus* indirectly lowered development time and increased adult mass and estimated finite rate of increase for *A. triseriatus*, probably due to release from density dependence. These patterns confirm the prediction of greater vulnerability of *A. aegypti*.

6. For both *Aedes* species, survivorship and estimated finite rate of increase were not differentially affected by interspecific vs. intraspecific competition. Estimated finite rates of increase achieved when in competition gave no indication of a strong competitive advantage for either species. For female *A. aegypti*, mass at adulthood and development time were more detrimentally affected by intraspecific vs. interspecific competition. For *A. triseriatus*, development time was more detrimentally affected by interspecific vs. intraspecific competition. These results provide, at best, only weak support for the predicted competitive advantage for *A. aegypti*.

7. We suggest that in some systems, prey behaviour patterns are more related to vulnerability to predation than to competitive ability.

Key-words: *Aedes aegypti*, *Aedes triseriatus*, aquatic insects, *Toxorhynchites rutilus*, trade-off between competition and predation.

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Introduction

Although competition and predation are often modelled and understood at the population or community level, it is the characteristics of individual organisms, such as body size (Wilbur 1988; Lawton 1991; Werner 1992, 1994) and behaviour (Woodward 1983; Pierce, Crowley & Johnson 1985; Sih 1986, 1987; Kohler & McPeek 1989; McPeek 1990) that determine the effects of these interactions at the population and community levels. In freshwater systems, in particular, behaviour pattern, including level of activity, kind of activity,

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and individual habitat use, have all been documented or suggested to influence vulnerability to predation (e.g. Woodward 1983; Pierce *et al.* 1985; Kats, Petranka & Sih 1988; Lawler 1989; Peckarsky & Wilcox 1989; Peckarsky & Penton 1989; Blois-Heulin *et al.* 1990; McPeek 1990; Skelly & Werner 1990; Skelly 1992), or competitive ability (e.g. Reynoldson, Gilliam & Jacques 1981; Woodward 1982; Morin & Johnson 1988; Ho, Ewert & Chew 1989; Werner 1992, 1994; Werner & Anholt 1993) of otherwise similar organisms. There appears to be a trade-off between competitive ability and vulnerability to predation, with highly active organisms having greater competitive ability, presumably due to greater ability to locate and harvest scarce resources, but also having greater vulnerability to predation, presumably due to greater encounter rate with, or detectability to predators (e.g. Werner & Anholt 1993; Werner 1994; Crowley & Hopper 1994). This behavioural trade-off has been studied in amphibian larvae (Woodward 1982, 1983; Morin 1983; Werner 1992, 1994) and in odonates (Pierce *et al.* 1985; Blois-Heulin *et al.* 1990), but the mechanisms producing this trade-off seem likely to operate for other aquatic organisms.

The connection between behaviour and vulnerability to predation is most obvious over short time scales. Over minutes or hours, greater activity increases probability of contact and detection by predators, resulting in greater death rate (Sih 1986; Lawler 1989; Juliano & Reminger 1992). Whether such behavioural traits affect survivorship over longer periods (e.g. days, weeks, lifetimes) depends on ontogenetic changes in mortality rate and the duration of exposure to a particular predator. Development rate may influence duration of exposure to a particular mortality regime, and total mortality due to predation may be lower if, for example, greater activity leads to faster growth and development and a size or stage refuge from predators (Wilbur 1988).

The hypothesized connection between activity and competitive ability probably is mediated via one component of resource competition, rate of harvest and depletion of resources (competitive effect, Werner 1994). Other components of competitive interactions (e.g. minimum resource intake requirements, efficiency) are likely to depend on both behaviour (e.g. foraging effort and efficiency) and on other traits (e.g. metabolic rate, Lawton 1991; Werner 1994), and this dependence may mean that behavioural differences in resource harvest rate and depletion do not inevitably lead to an overall competitive advantage. Proximate effects of activity level on harvest rate are likely to be most obvious for components of population growth and fitness (e.g. development time, size at maturity, growth rate: Morin & Johnson 1988; Werner 1991, 1994). Whether such effects ultimately lead to an overall competitive advantage (i.e. at the level of population growth rate) depends on how fitness components are jointly affected and how they are interrelated.

Based on these lines of reasoning, behaviour may serve as an important and common mechanistic basis for the outcome of many animal species interactions, but further empirical study is necessary to support this view. If behavioural traits are a major determinant of competitive ability, vulnerability to predation, and the trade-off between the two, it should be possible to predict the outcomes of species interactions based on quantifiable behavioural traits, particularly if the species in question are similar in other traits (size, morphology, life cycle). We chose to investigate the general hypothesis that behaviour is a major determinant of competitive ability and vulnerability to predation by a combination of behavioural observations, a short-term predation experiment, and a long-term competition and predation experiment using three container-dwelling mosquitoes: *Aedes aegypti* (L.), *Aedes triseriatus* (Say), and the predator *Toxorhynchites rutilus* (Coq.).

EXPERIMENTAL SYSTEM

In the south-eastern United States, larvae of *A. aegypti* (an introduced species), and *A. triseriatus* (a native species) co-occur primarily in discarded, water-filled tyres (Christophers 1960; Wilton 1968; Ho *et al.* 1989). *Toxorhynchites rutilus* larvae develop in these same types of containers, and prey upon other insects including *A. aegypti* and *A. triseriatus*. *T. rutilus* is primarily a tactile, ambush-style predator (Russo 1986; Linley 1990).

Some of the important assumptions of the hypothesis are met by this system. Larval resource requirements, sizes, morphologies, and life cycles of *A. aegypti* and *A. triseriatus* are very similar (Wilton 1968; Ho *et al.* 1989; Merritt, Dadd & Walker 1992); hence, resource competition may be important where larvae co-occur, and non-behavioural differences influencing species interactions are likely to be minimal. Short-term vulnerability of mosquito larvae to predation by *Toxorhynchites* spp. depends at least in part on prey behaviour (Rubio *et al.* 1980; Chambers 1985; Russo 1986; Juliano & Reminger 1992).

SPECIFIC PREDICTIONS

Based on the hypothesis that behaviour is a mechanistic determinant of species interactions we predict that: (i) the *Aedes* species that exhibits greater activity, greater allocation of time to foraging and greater time foraging in more productive areas will have a competitive advantage over its congener when measured proximately as competitive effects on fitness components (survival, development time, adult size) and ultimately as competitive effects on population growth; (ii) the *Aedes* species that, in the presence of *T. rutilus*, spends more time in activities or places that entail greater risk of predation will have lower short-term (over minutes) and long-term (over days or

weeks) survivorship when exposed to this predator; and (iii) the *Aedes* species with greater competitive ability will also be more vulnerable to predation.

Methods

COLLECTION AND MAINTENANCE OF MOSQUITOES

Aedes larvae and pupae were field collected near Florida Medical Entomology Laboratory, Vero Beach, FL, and colonies were established and maintained using methods described by Juliano (1989). *T. rutilus* were field collected as eggs and first instar larvae from tyres near Ashland, VA, and raised at 22 °C, L:D 17:7 on a diet of *Aedes* larvae (primarily *A. triseriatus*).

Experiment 1: Behaviour of A. aegypti *and* A. triseriatus

Eggs of *A. triseriatus* (F_2 in the laboratory) and *A. aegypti* (F_{5-10} in the laboratory) were hatched synchronously (for methods, see Juliano 1989). Twelve hours after hatching, first instar larvae were placed in 250 mL plastic beakers (88 larvae per 200 mL water), given a single feeding of 0·5 mg liver powder per larva, and reared at 24 °C, L:D 17:7.

Individual larvae were placed in 50 mL beakers (30 mL tap water, initially at 24 °C) and after 5 min acclimation, positions and activities of individuals were recorded every minute for 30 min, using instantaneous scan censuses (Martin & Bateson 1986; Juliano & Reminger 1992; Juliano, Hechtel & Waters 1993). Behaviours were categorized into activities and positions (Juliano & Reminger 1992; Juliano *et al.* 1993). Activities included: (i) thrashing—moving through the water via vigorous flexions of the body; (ii) filtering— removal of particles from the water using currents generated with the mouth parts, usually with slow movement through the water; (iii) browsing—brushing solid surfaces with the mouth parts, usually with movement along the surface; (iv) resting—not feeding or moving. Positions were defined as: (i) surface—spiracular siphon at the water's surface; (ii) wall—below the surface and within 1 mm of the wall; (iii) bottom— within 1 mm of the bottom and >1 mm from the wall; (iv) middle—not at the surface, wall, or bottom.

First or second instar *A. aegypti* and *A. triseriatus* were observed (10 at a time, in approximately equal proportions) with the species of each larva unknown to the observer. Different rates of development made it necessary to observe 3rd and 4th instars of each species separately (up to 15 at a time). A total of 80 *A. triseriatus* and 77 *A. aegypti* larvae were observed (*c.*20 larvae per instar for each species). For each larva, proportion of observations in each position or activity were arcsine-$\sqrt{}$ transformed and analysed using mul-

tivariate analysis of variance (MANOVA) with SPECIES, STAGE (early = 1st and 2nd instars, late = 3rd and 4th instars), and INTERACTION as effects. For significant MANOVA effects, individual variables were further analysed using analyses of variance (ANOVA) with critical α-values adjusted to account for four tests per effect (Bonferroni method: individual α = 0·05/4 tests = 0·0125). In the interests of brevity, *F* and *P*-values are omitted, and only statistical significance of univariate tests is reported.

PREDICTION OF COMPETITIVE ABILITY

We believe that feeding behaviours are the activities most closely related to ability to compete for resources, and therefore predict a competitive advantage for the species that allocates greater time to feeding. We further expect that browsing is usually more profitable than filtering because browsing is likely to lead to ingestion of larger, more profitable particles (e.g. protozoans, attached microbes) (Merritt *et al.* 1992) and because hungry *A. triseriatus* significantly increase browsing, but not filtering (Juliano *et al.* 1993), suggesting that browsing is more likely to yield a greater return. Thus, we predict a competitive advantage for the species that allocates more foraging time to browsing. Overall activity level (i.e. time not resting) may also contribute to competitive advantage (e.g. Werner 1991, 1994). Finally, we predict a competitive advantage for the species that spends more time at the bottom, where resources are likely to be more concentrated (Merritt *et al.* 1992).

Experiment 2: Behaviour of A. aegypti *and* A. triseriatus *in the presence of* T. rutilus

Aedes eggs were hatched synchronously and placed in 250 mL beakers (100 larvae per 200 mL water). Other rearing conditions were as in Experiment 1. For observations, six 50 mL beakers were filled with 30 mL tap water (initially at 24 °C). One *T. rutilus* larva (starved 16 h) and one *Aedes* larva were placed in each beaker and allowed to acclimate for 5 min, with *T. rutilus* larvae isolated in vertical, open-ended tubes. Trials began with the simultaneous removal of all isolation tubes (Juliano & Reminger 1992). Equal numbers of both species were observed simultaneously. Early (1st and 2nd) and late (3rd and 4th) instar *Aedes* were observed with 2nd or 3rd instar, and 3rd or 4th instar *T. rutilus*, respectively.

Trials were videotaped from directly overhead, and behaviour of larvae was quantified from video tapes using instantaneous scan censuses similar to those described for Experiment 1 (MANOVA indicated no significant differences between simultaneous live vs. video-taped observations). Because predation ended some trials, we recorded activity and position of larvae every 15 s for 7·5 min, for a maximum of 30 observations for each larva. Behaviour patterns of larvae

captured prior to obtaining 30 observations, were analysed only if there were ≥ 10 observations. We obtained behavioural data from 49 *A. aegypti* and 66 *A. triseriatus*, and of these 115 data points, only 11 were based on less than 30 observations per larva.

Behavioural data from Experiment 2 were analysed in the same way as those from Experiment 1 in order to test for interspecific differences in behaviour in the presence of the predator. Because the two experiments used different protocols, we did not test for significant changes in behaviour in response to the predator (i.e. between experiments). Our goal is to determine whether the two species differ under these two different sets of conditions, and to use any interspecific differences to predict the outcomes of interspecific interactions.

PREDICTION OF VULNERABILITY TO PREDATION

Among activities, thrashing entails the greatest risk of predation and resting the least, whereas among positions, the bottom entails the greatest risk and the surface the least (Juliano & Reminger 1992). With this information it may be possible to predict interspecific differences in vulnerability to predation based on behaviour; however, ambiguities can arise (Juliano *et al.* 1993). If, for example, one species exhibits higher frequencies of both resting and thrashing than another species, it would be difficult to predict relative vulnerability to predation (Juliano *et al.* 1993). Our solution to this problem is to combine information on behaviour and estimated risks of different behaviours into an index that quantifies total behavioural risk of predation (Juliano *et al.* 1993). We used information on riskiness of activities and positions (Juliano & Reminger 1992; Juliano *et al.* 1993), and our observations of behaviour in the presence of *T. rutilus* (Experiment 2) to calculate the risk scores (*RS*) derived by Juliano *et al.* (1993), from which we predict relative risk of predation for the two species. Details on the construction of the index *RS* are fully described by Juliano *et al.* (1993), and are omitted here. *RS* takes into account both the relative risk of each behaviour and the frequency with which each behaviour occurs, and varies from -1 to $+1$, with greater values indicating behaviour patterns that entail greater risk of predation. We calculated these values for activities (RS_A) and positions (RS_P) separately, and for early and late stage larvae separately, and analysed these using MANOVA and ANOVA, with SPECIES, STAGE and INTERACTION as model effects. Significantly greater *RS* for one species leads to predictions of greater vulnerability to predation over both the short term (lower survival times in Experiment 2) and the long term (lower proportion survival in Experiment 3) for that species.

SHORT-TERM VULNERABILITY TO PREDATION

From the video recordings in Experiment 2, we determined the survival time of each larva in the presence of *T. rutilus*. We tested whether survival time distributions within stages (early, late) differed between the species using the Wilcoxon failure time test (Fox 1993; SAS Institute Inc. 1987; procedure LIFETEST).

We emphasize that our estimates of the riskiness of different behaviours were derived from an independent experiment (Juliano & Reminger 1992), rendering our prediction of survival time from behavioural data noncircular.

Experiment 3: Competition and long-term vulnerability to predation

Fallen white oak (*Quercus alba* L.) leaves were collected at Parklands Foundation Forest Preserve near Lexington, IL in August 1991. Leaves were broken into $c.1\,\text{cm}^2$ pieces, dried for 48 h at 60 °C, and 3-g allotments were soaked in 320 mL tap water in 400 mL plastic beakers for 3 days prior to addition of larvae. Leaves provided a substrate for growth of microbes, the primary food of larvae. Eggs of *A. triseriatus* and *A. aegypti* were hatched synchronously as in Experiment 1. The design of the experiment is summarized in Table 1. For each *Aedes* species, there were eight treatment combinations resulting from three factors: COMPETITOR (alone vs. with the other species); PREDATOR (0 vs. 1 *T. rutilus* larva, initially in the first instar); and DENSITY (100 vs. 200 *Aedes* per beaker) (Table 1). For a species, the DENSITY effect is a measure of whether density dependence (competition) influences performance. The DENSITY × COMPETITOR interaction tests whether effects of intra- and interspecific competition are the same (i.e. whether doubling density with conspecifics is equivalent to doubling density with heterospecifics). Beakers containing each species alone were designated as treatments AA for *A. aegypti* and TT for *A. triseriatus*. Beakers containing both species were designated treatments AT for *A. aegypti* and TA for *A. triseriatus*.

This experiment was done at 24 °C, L:D 17:7 and was monitored daily for *Aedes* adults and *T. rutilus* mortality (one *T. rutilus* larva died and was replaced with another of the same instar and similar size). Adult *Aedes* were dried (60 °C for ≥ 48 h), and weighed to the nearest 0·1 μg. From this experiment we obtained data for *A. aegypti* and *A. triseriatus* on fitness components: survival to adulthood (sexes pooled); median days to eclosion for each sex; and mean adult mass for each sex. We also calculated a composite index of performance based on r' (Livdahl 1984; Livdahl & Sugihara 1984), which estimates the realized per capita rate of population change ($dN/Ndt = r$, the exponential growth rate) within each replicate. We chose as our composite index of population performance $\lambda' = \exp(r')$ (analogous to the finite rate of increase

Table 1. Design of Experiment 3. In each column are the number of larvae of each species initially present in 12 different treatment combinations. All three species began the experiment as first instar larvae. Each of the 12 treatment combinations was replicated four times, for a total of 48 beakers. Analysis for each *Aedes* species included only those treatment combinations containing that species (32 beakers for each species)

Species	Low density (100 total *Aedes*)						High density (200 total *Aedes*)					
T. rutilus	0	1	0	1	0	1	0	1	0	1	0	1
A. aegypti	100	100	50	50	0	0	200	200	100	100	0	0
A. triseriatus	0	0	50	50	100	100	0	0	100	100	200	200

$\lambda = \exp(r)$, Pianka 1988). In demographic analyses, λ is preferable to r because λ is estimable even if no individuals survive to reproductive age ($\lambda = 0$), whereas r is unestimable ($r = -\infty$) in that circumstance (Lenski & Service 1982). The same relationship holds for λ' and r'.

The composite index λ' was calculated for each species within each replicate as follows:

$$\lambda' = \exp(r') = \exp\left(\frac{\ln\left[(1/N_o)\sum_x A_x f(w_x)\right]}{D + \left[\sum_x x A_x f(w_x)/\sum_x A_x f(w_x)\right]}\right)$$

where N_o is the original number of females of that species (assumed to be 50% of the initial cohort), A_x is the number of females eclosing on day x, w_x is the mean dry mass of females eclosing on day x, $f(w_x)$ is the function relating production of female progeny to female dry mass, and D is the time between adult eclosion and reproduction. A_x and w_x were determined for each replicate; D was assumed to be 12 days for both *Aedes* species (personal observation). Regressions relating female progeny to dry mass at eclosion were:

A. aegypti $\quad f(w_x) = 17\cdot11 + 16\cdot59(w_X^{0\cdot765})$

$$r^2 = 0\cdot102 \quad n = 57$$

(based on Colless & Chellapah 1960)

A. triseriatus $\quad f(w_x) = (1/2)\exp(4\cdot505 + (1\cdot348\ln(w_x)))$ $\quad r^2 = 0\cdot471 \quad n = 30$

(unpublished data for the population from Vero Beach). These low r^2 values indicate that there is considerable unexplained variation in fecundity, hence our ability to predict rate of increase is limited (see Discussion).

Survivorship was analysed as a three-way factorial ANOVA (SAS Institute Inc. 1987; PROC GLM) using a $^3\sqrt{}$ transformation to meet ANOVA assumptions. For *A. triseriatus*, three-way factorial ANOVA was also used for median days to eclosion (inverse transformed, hence eclosion rate) and mean mass at eclosion for each sex. For *A. aegypti* three-way ANOVA was not possible for median days to eclosion or mean adult mass due to low survival in PREDATOR treatments, and we instead performed two-way ANOVAs on no-predator treatments using DENSITY, COMPETITOR and INTERACTION as the model effects.

Significant main effects and interactions were further analysed using specific pairwise comparisons of least squares means (SAS Institute Inc. 1987) at an experiment-wise $\alpha = 0\cdot05$ (Bonferonni method). For λ', no transformation yielded data that met ANOVA assumptions; hence three-way randomization ANOVAs (Manly 1991a;b) and comparison of 95% confidence intervals generated using randomization methods (Manly 1991a;b) were used.

Results

Experiment 1: Behaviour of A. aegypti *and* A. triseriatus

Activity. MANOVA indicated significant STAGE (Wilk's $\Lambda = 0\cdot5914$, df $= 4{,}149$, $P = 0\cdot0001$), SPECIES (Wilk's $\Lambda = 0\cdot6206$, df $= 4{,}149$, $P = 0\cdot0001$) and INTERACTION (Wilk's $\Lambda = 0\cdot8023$, df $= 4{,}149$, $P = 0\cdot0001$) effects on activity pattern. Hence, interspecific differences in activity patterns were not consistent across stages. *A. aegypti* spent significantly more time browsing than did *A. triseriatus* during early instars, but the proportions did not differ in the late instars (Fig. 1). The proportion of time spent browsing by *A. aegypti* remained constant across STAGE, but increased significantly from early to late instars for *A. triseriatus* (Fig. 1). *A. triseriatus* filtered significantly more than did *A. aegypti* during the late instars (Fig. 1), but time spent filtering during early instars did not differ (Fig. 1). *A. triseriatus* always spent significantly more time resting than did *A. aegypti* and STAGE had no effect on time spent resting by either species (Fig. 1). Proportion of time spent thrashing by each species did not differ in early instars, but was significantly lower for in *A. triseriatus* vs. *A. aegypti* during late instars (Fig. 1).

Position. MANOVA indicated significant STAGE (Wilk's $\Lambda = 0\cdot6788$, df $= 4{,}149$, $P = 0\cdot0001$), SPECIES (Wilk's $\Lambda = 0\cdot5990$, df $= 4{,}149$, $P = 0\cdot0001$) and INTERACTION (Wilk's $\Lambda = 0\cdot8659$, df $= 4{,}149$, $P = 0\cdot0002$) effects. Hence, interspecific differences in pattern of positions occupied were not consistent across stages. *A. aegypti* always spent significantly more time at the bottom than did *A. triseriatus*,
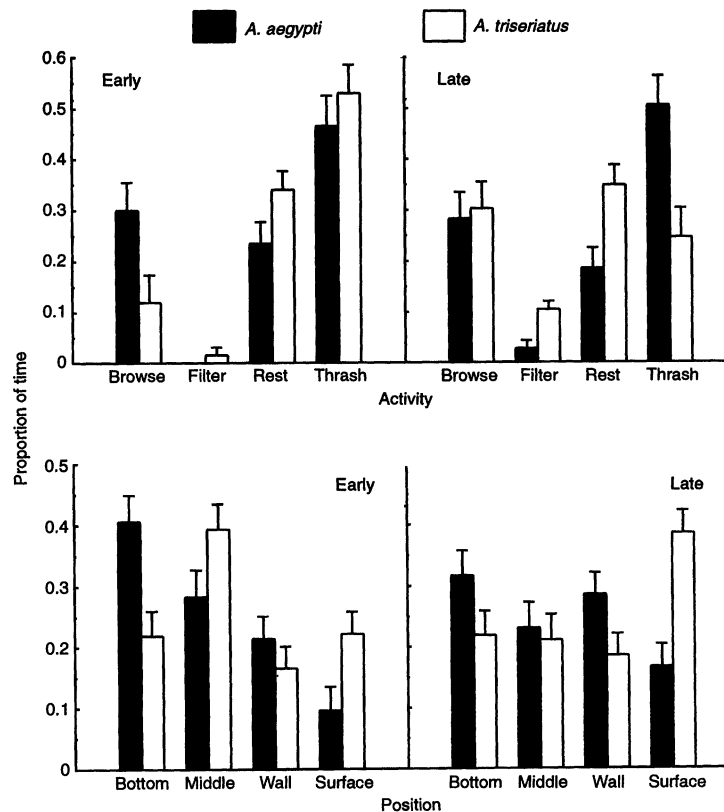
Fig. 1. Estimated proportions of time spent in different activities and positions by *Aedes aegypti* and *Aedes triseriatus* in the absence of the predator *Toxorhynchites rutilus* (mean + 2 SE). Sample sizes: *A. aegypti, n* = 36 (early), *n* = 40 (late); *A. triseriatus, n* = 40 (early), *n* = 40 (late).

especially in early instars (Fig. 1). *A. triseriatus* spent significantly more time in the middle than *A. aegypti* during the early stage, but no interspecific differences were found in the late stage (Fig. 1). *A. triseriatus* spent significantly more time in the middle during the early stage than the late stage. Time spent in the middle by *A. aegypti* did not differ between stages (Fig. 1). *A. aegypti* spent more time at the wall than did *A. triseriatus* during both stages. *A. triseriatus* spent more time at the surface than *A. aegypti* during both stages (Fig. 1).

PREDICTION OF COMPETITIVE ABILITIES

The two species differ in frequencies of feeding behaviours, but the differences depend on instar, and allocation of foraging time to filtering vs. browsing sometimes differs. For early instars, *A. aegypti* spends significantly more time browsing than does *A. triseriatus* (Fig. 1) and time spent filtering does not differ. For late instars, time spent browsing does not differ, and *A. triseriatus* spends significantly more time filtering (Fig. 1). Because browsing is likely to be the more profitable foraging mode, any competitive advantage due to allocation of feeding time probably falls to *A. aegypti*. Overall activity level (i.e. time not resting) is also greater for *A. aegypti*, which may also contribute to competitive advantage. In conjunction with these differences in activity, there are interspecific

differences in positions, with significantly greater time at the bottom for *A. aegypti* compared to *A. triseriatus*, which also leads to the prediction that *A. aegypti* should have a competitive advantage.

Experiment 2: Behaviour of A. aegypti *and* A. triseriatus *in the presence of* T. rutilus

Activity. MANOVA indicated significant STAGE (Wilk's $\Lambda = 0.6495$, df $= 4,108$, $P = 0.0001$), SPECIES (Wilk's $\Lambda = 0.4474$, df $= 4,108$, $P = 0.0001$) and INTERACTION (Wilk's $\Lambda = 0.8958$, df $= 4,108$, $P = 0.0174$) effects on activity patterns in the presence of *T. rutilus*. Hence, interspecific differences in activity patterns were not consistent across stages, as was true in the absence of *T. rutilus*. *A. triseriatus* filtered significantly more than did *A. aegypti* during both early and late instars, but the magnitude of the difference was greater for late instars (Fig. 2). *A. triseriatus* spent significantly more time resting than did *A. aegypti* and STAGE had no effect on resting (Fig. 2). Proportion of time spent thrashing was significantly lower for *A. triseriatus* than for *A. aegypti*, and was significantly greater in early instars vs. late instars (Fig. 2). Browsing was uniformly rare for both species (Fig. 2). The major interspecific differences in activity patterns (less thrashing and more resting and filtering by *A. triseriatus*) were similar, but not identical, whether *T. rutilus* was present or not (compare Figs 1 and 2).
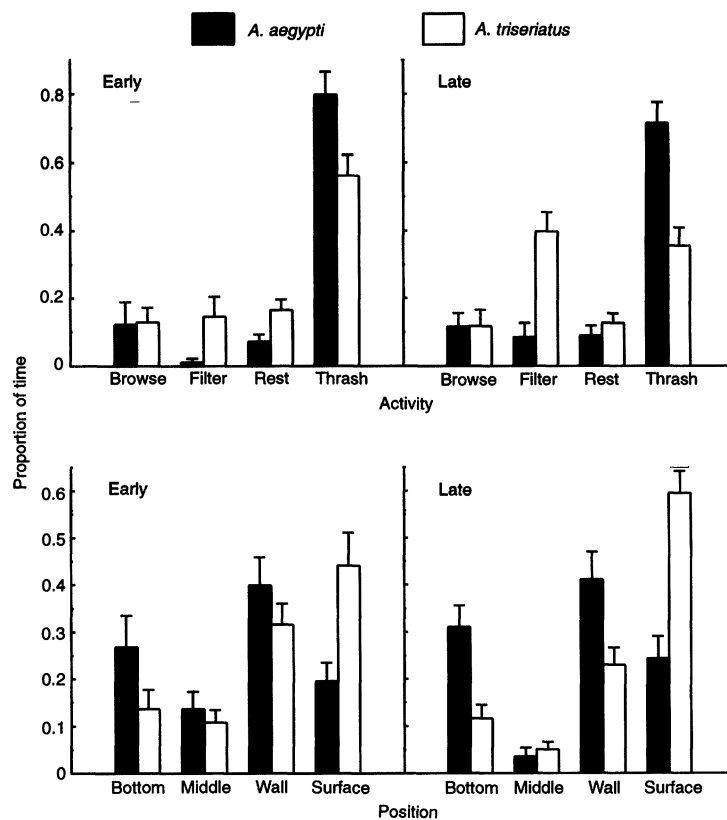
Fig. 2. Estimated proportions of time spent in different activities and positions by *Aedes aegypti* and *Aedes triseriatus* in the presence of the predator *Toxorhynchites rutilus* (mean + 2 SE). Sample sizes: *A. aegypti, n* = 26 (early), *n* = 23 (late); *A. triseriatus, n* = 34 (early), *n* = 32 (late).

Position: MANOVA indicated significant STAGE (Wilk's Λ = 0·6672, df = 4,108, *P* = 0·0001) and SPECIES (Wilk's Λ = 0·5181, df = 4,108, *P* = 0·0001) effects on pattern of positions occupied. The effect of INTERACTION (Wilk's Λ = 0·9373, df = 4,108, *P* = 0·1329) was not significant in the presence of *T. rutilus*. Hence, interspecific differences in patterns of positions occupied were consistent across stages. *A. aegypti* spent significantly more time at the bottom than did *A. triseriatus*, as was true in the absence of *T. rutilus* (compare Figs 1 and 2). *A. triseriatus* spent significantly more time at the surface than *A. aegypti*, and late instar larvae spent more time at the surface than did early instar larvae (Fig. 2). Time spent in the middle was unrelated to species, and was significantly less for late vs. early instars (Fig. 2). *A. aegypti* spent significantly more time at the wall than did *A. triseriatus* (Fig. 2). The major interspecific differences in positions occupied (more time at the bottom and wall and less time at the surface for *A. aegypti*) were similar, but not identical, whether *T. rutilus* was present or not (compare Figs 1 and 2).

PREDICTION OF VULNERABILITY TO PREDATION

MANOVA of RS_P and RS_A indicated significant STAGE (Wilk's Λ = 0·4881, df = 4,110, *P* = 0·0001), SPE-CIES (Wilk's Λ = 0·5853, df = 4,110, *P* = 0·0001)

and INTERACTION (Wilk's Λ = 0·8759, df = 4,110, *P* = 0·0007) effects. Thus, interspecific differences in risk scores were not consistent across stages. For both early and late instar larvae, RS_A was significantly greater for *A. aegypti* than for *A. triseriatus*, but the difference for late instar larvae was much greater than that for early instar larvae (Fig. 3). In pairwise com-
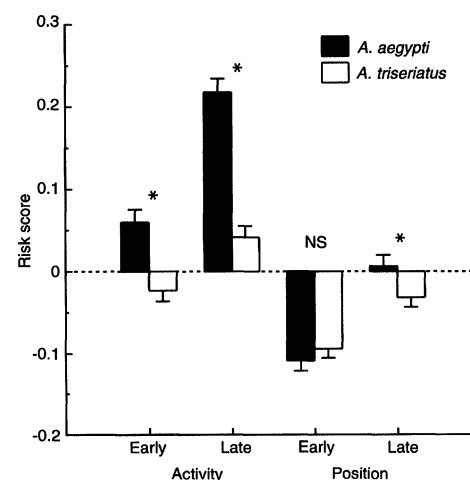

Fig. 3. Risk scores for positions and activities of *Aedes aegypti* and *Aedes triseriatus* in the presence of the predator *Toxorhynchites rutilus* (mean + 2 SE). Sample sizes: *A. aegypti, n* = 26 (early), *n* = 23 (late); *A. triseriatus, n* = 34 (early), *n* = 32 (late). Pairwise differences significant at experiment-wise α = 0·05 are indicated by *.

parisons, the interspecific difference in RS_P for late instar larvae was also significant, but that for early instar larvae was not (Fig. 3). Thus, it is clear that behaviour patterns of *A. aegypti* should lead to greater risk of predation by *T. rutilus* than should those of *A. triseriatus*. This prediction is clearest based on activity patterns, but the same trend is apparent in patterns of position in late instar larvae (Fig. 3). We therefore predict that short-term and long-term vulnerability to predation should be greater for *A. aegypti* than for *A. triseriatus*.

Short-term vulnerability to predation by T. rutilus

For both early and late instar larvae, survivorship declined significantly more rapidly for *A. aegypti* than for *A. triseriatus* (Fig. 4), indicating that short-term vulnerability to predation by *T. rutilus* was greater for *A. aegypti* than for *A. triseriatus*. Median survival times were greater than 3600 s for both early and late instar *A. triseriatus*, whereas median survival times were 2931 s and 570 s for early and late instar *A. aegypti*, respectively (Fig. 4). These results are consistent with the prediction of interspecific differences in short-term vulnerability to predation derived from our behavioural data.

Experiment 3: Competition and long-term vulnerability to predation by T. rutilus

Survival. For *A. aegypti*, a significant three–way interaction (Table 2) indicated that the effects of DEN-SITY × COMPETITOR combinations depended on the presence or absence of *T. rutilus* (Fig. 5). *A. aegypti* survival did not differ significantly between the different levels of DENSITY and COMPETITOR when *T. rutilus* was present, primarily because virtually no *A. aegypti* survived in the presence of the predator

(Fig. 5). When *T. rutilus* was absent, *A. aegypti* survival at low density was significantly greater with *A. triseriatus* (AT) vs. with conspecifics only (AA) (Fig. 5). When *T. rutilus* was absent, survival at high density (where competition should be important) was very low and unaffected by competitor treatments (Fig. 5).

For *A. triseriatus*, PREDATOR × DENSITY interaction significantly affected survival (Table 2). With *T. rutilus* absent, *A. triseriatus* survival was significantly greater at low density vs. high density (Fig. 5), whereas with *T. rutilus* present, *A. triseriatus* survival was slightly, but not significantly, greater at high density. The DENSITY × COMPETITOR interaction was also significant (Table 2). At high density, *A. triseriatus* survival was the same whether competing with *A. aegypti* (TA) or with conspecifics only (TT), but at low density, survival was greater when competing with *A. aegypti* (TA) vs. when competing with conspecifics only (TT) (Fig. 5).

Mean mass at eclosion. In the absence of *T. rutilus*, only COMPETITOR significantly affected mean masses of both male ($F_{1,7} = 23·84$, $P = 0·0018$) and female *A. aegypti* ($F_{1,11} = 7·09$, $P = 0·0221$). Female mass was greater when competing with *A. triseriatus* (mean ± 2 SE $= 0·212 \pm 0·026$ mg) vs. when competing only with conspecifics ($0·160 \pm 0·028$ mg). The result for males should be interpreted with caution due to the absence of size estimates for males from high density – AT treatments; however, at low density, male mass was also greater when competing with *A. triseriatus* ($0·148 \pm 0·012$ mg) vs. when competing with only conspecifics ($0·106 \pm 0·012$ mg).

For *A. triseriatus*, only PREDATOR and DEN-SITY significantly affected mean mass of both males ($F_{1,20} = 102·68$ and $9·29$, respectively, $P = 0·0001$ and $0·0063$, respectively) and females ($F_{1,21} = 103·38$ and
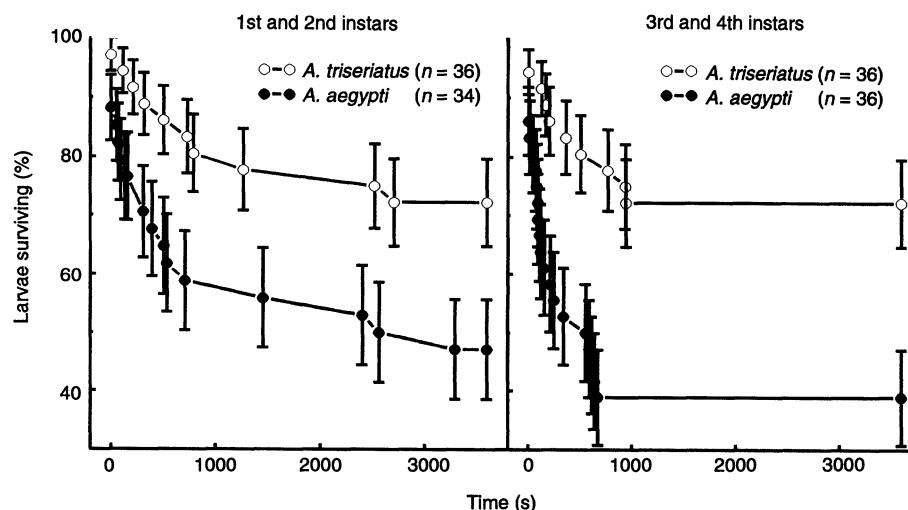
Fig. 4. Survivorship curves ($\pm$ SE) for *Aedes aegypti* and *Aedes triseriatus* in Experiment 2. Survivorship curves for the two species differ significantly for both early (Wilcoxon $\chi^2 = 5·669$, df $= 1$, $P = 0·0173$) and late (Wilcoxon $\chi^2 = 9·958$, df $= 1$, $P = 0·0016$) instar larvae.

Table 2. ANOVA for effects of COMPETITOR, DENSITY and PREDATOR on survival ($^3\sqrt{}$-transformed) for *A. aegypti* and *A. triseriatus*

Source	df	A. aegypti		A. triseriatus	
		F	P	F	P
COMPETITOR	1	0·45	0·5085	3·65	0·0680
DENSITY	1	64·92	0·0001	98·95	0·0001
COMP. × DENS.	1	0·64	0·4340	8·94	0·0064
PREDATOR	1	89·36	0·0001	75·56	0·0001
PRED. × COMP.	1	9·14	0·0059	4·00	0·0571
PRED. × DENS.	1	25·91	0·0001	165·32	0·0001
PRED. × COMP. × DENS.	1	4·44	0·0458	0·50	0·4883
Error mean square	24	0·0133		0·0039	

Table 3. Randomization ANOVA (Manly 1991a, b) for effects of PREDATOR, COMPETITOR, and DENSITY on λ' for *A. aegypti* and *A. triseriatus*. Significance levels are determined from the proportion of randomizations (out of 1000) in which sum of squares (as percentage of total) for a factor exceeded that observed for that factor in the real data set

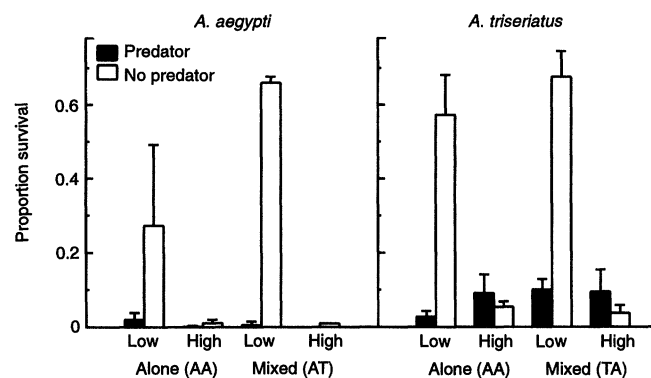| Source	df	A. aegypti		A. triseriatus	
		Observed SS (%)	P	Observed SS (%)	P
COMPETITOR	1	1·29	0·659	1·55	0·412
DENSITY	1	2·67	0·298	3·01	0·221
COMP. × DENS.	1	1·22	0·667	1·23	0·536
PREDATOR	1	58·22	0·001	1·41	0·412
PRED. × COMP.	1	6·50	0·155	1·35	0·487
PRED. × DENS.	1	0·10	0·722	12·55	0·005
PRED. × COMP. × DENS.	1	0·04	0·746	1·52	0·384
Error	24	29·95		77·38	

Fig. 5. Proportion of larvae surviving to adulthood (mean + 2 SE) for *Aedes aegypti* and *Aedes triseriatus* in Experiment 3. For both species, each mean is based on *n* = 4 replicates.

23·54, respectively, *P* = 0·0001 for both). In both sexes, mean mass was greater at low density vs. high density, and was greater when *T. rutilus* was present vs. when *T. rutilus* was absent (Fig. 6). All other model effects were non-significant for *A. triseriatus*.

Median days to eclosion. In the absence of *T. rutilus*, *A. aegypti* female eclosion rate (= 1/median days to eclosion) was significantly affected only by DENSITY ($F_{1,11}$ = 14·84, *P* = 0·0027) and COMPETITOR ($F_{1,11}$ = 42·99, *P* = 0·0001). Eclosion rate of *A.*

aegypti females was greater at low density (mean ± 2 SE = 0·046 ± 0·006 day^{-1}) vs. high density (0·028 ± 0·006 day^{-1}), and greater when competing with *A. triseriatus* (0·053 ± 0·006 day^{-1}) vs. when competing with only conspecifics (0·022 ± 0·007 day^{-1}). There were no significant effects on eclosion rate of *A. aegypti* males.

For *A. triseriatus* females PREDATOR, DENSITY and COMPETITOR all significantly affected eclosion rate ($F_{1,21}$ = 32·50, 10·00, and 5·62, respectively, *P* = 0·0001, 0·0047, and 0·0274, respectively) but no
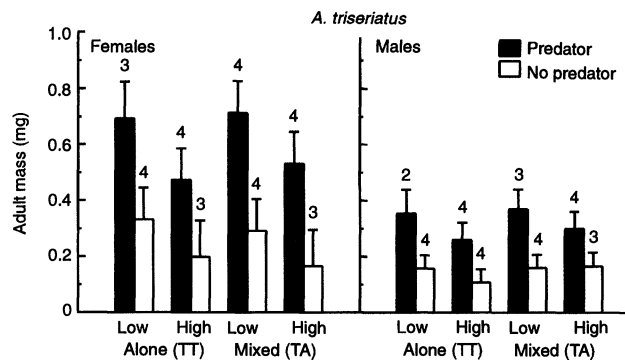
Fig. 6. Mean dry mass (mean + 2 SE) of adults of *Aedes triseriatus* from Experiment 3. Means are averages of means from replicates yielding adults. Sample sizes are indicated above the error bars.

interactions were significant. Females eclosed significantly sooner when predators were present vs. when predators were absent, at low vs. at high density, and when competing only with conspecifics (TT) vs. when competing with *A. aegypti* (TA) (Fig. 7).

For *A. triseriatus* males, PREDATOR × COMPETITOR interaction significantly affected eclosion rate ($F_{1,20} = 11·48$, $P = 0·0029$). In the absence of predators, *A. triseriatus* males eclosed significantly sooner when competing with conspecifics only (TT) vs. when competing with *A. aegypti* (TA) (Fig. 7). When a predator was present, there was no difference in time to eclosion of males in TA and TT treatments (Fig. 7). DENSITY also had a significant effect on eclosion rate of *A. triseriatus* males ($F_{1,20} = 34·61$, $P = 0·0001$), with males eclosing significantly sooner at low density vs. at high density (Fig. 7).

Composite index of fitness (λ'): For *A. aegypti*, λ' was significantly affected only by PREDATOR (Table 2), and was greater in no-predator vs. predator treatments (Fig. 8). When predators were absent and density was low, λ' was not significantly different from 1·0 (population stable), whereas when predators were absent and density was high, λ' was significantly less than 1·0 (population declining). With *T. rutilus* present, regardless of density, λ' was significantly below 1·0 and not significantly greater than 0 (Fig. 8),

indicating rapid population decline. No other effects were significant in three-way ANOVA for *A. aegypti*.

For *A. triseriatus*, DENSITY × PREDATOR interaction significantly affected λ' (Table 2). At low density, regardless of predation, λ' did not differ significantly from 1·0 (Fig. 8). In contrast, at high density, λ' was greater when *T. rutilus* was present vs. when *T. rutilus* was absent (Fig. 8). Predation actually increased population performance at high density. At high density, without predation, λ' was significantly below 1·0, indicating population decline, whereas at high density, with predation, λ' was not significantly different from 1·0 (Fig. 8).

Discussion

Our experiments demonstrate that interspecific differences in behaviour of *Aedes triseriatus* and *A. aegypti* are closely related to vulnerability to predation by *Toxorhynchites rutilus* at all levels of analysis (short-term and long-term survival and estimated rate of population change). The relationship of behaviour to competitive ability is only weakly supported in these experiments.

Foraging time and location are likely to affect competitive ability, and based on the interspecific differences in foraging activity and location, we expect *A. aegypti* to have a competitive advantage over *A. tri-*
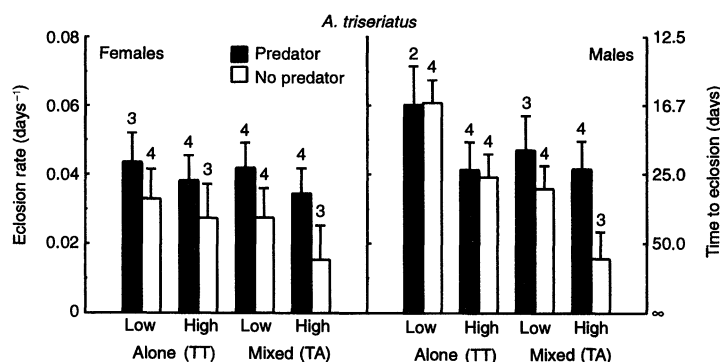
Fig. 7. Eclosion rate (= 1/median days to eclosion) (mean + 2 SE) of adults of *Aedes triseriatus* from Experiment 3. Means are averages of medians from replicates yielding adults. Sample sizes are indicated above the error bars.
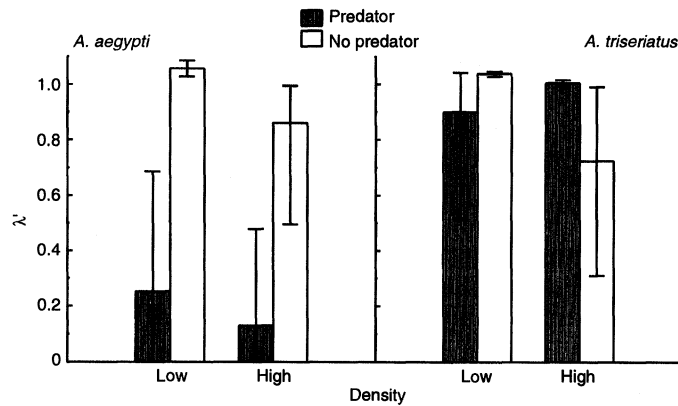
Fig. 8. Means $\pm$ 95% confidence intervals (generated by randomization, see Manly 1991a;b) for λ', the estimated finite rate of increase, for *Aedes aegypti* and *Aedes triseriatus* in Experiment 3. Because COMPETITOR (i.e. competing with the other species or with conspecifics only) was not involved in any significant effects (Table 3), means are given for PREDATOR × DENSITY combinations pooling across levels of COMPETITOR. For all groups, $n = 8$.

seriatus, primarily due to greater browsing at the bottom and greater movement. If this advantage was real we would expect *A. aegypti* to perform better than *A. triseriatus* at high combined density. This difference would result in *A. aegypti* maintaining positive population growth at high density, while population growth rate of *A. triseriatus* at high combined density would be $\leqslant 0$. Alternatively, the impact of *A. aegypti* on *A. triseriatus* may be greater than the impact of *A. triseriatus* on itself (i.e. interspecific competition is stronger than intraspecific competition).

In the competition experiment, performance of *A. aegypti* at high density was not, however, greater than that of *A. triseriatus*. Our composite index of performance, λ', was < 1·0 (i.e. populations were declining) for both species at high density (see Fig. 8). There is some evidence for differential impacts of interspecific vs. intraspecific competition on some fitness components. For *A. aegypti* in the absence of predation, mass at adulthood and time to metamorphosis were less detrimentally affected by addition of *A. triseriatus* than by addition of conspecifics. However, the impacts of interspecific and intraspecific competition on survivorship and λ' were the same for *A. aegypti* (see Figs 5 and 8). For *A. triseriatus* in the absence of predation, time to metamorphosis was more detrimentally affected by addition of *A. aegypti* than by addition of conspecifics. However, at low density without predation, survival of *A. triseriatus* was actually better when *A. aegypti* was present than when only conspecifics were present. All other fitness components and λ' were equally affected by interspecific and intraspecific competition.

Competitive advantage falls to the species that maintains a stable or growing population while its competitor's population declines (Pianka 1988). The composite variable λ' estimates a population's realized finite rate of increase, and probably gives the best indication of population performance in the competitive situation established in the experiment. Though only an approximation, λ' synthesizes these conflicting components in a biologically meaningful way. Our estimates of λ' are imprecise because of the low r^2s relating fecundity to mass (see Methods); however, this imprecision affects inferences of competitive ability based on individual fitness components (e.g. mass) as well. Fitness components need not be linearly related to population growth and may be negatively correlated (Livdahl & Sugihara 1984; Juliano 1989; Fisher, Bradshaw & Kammeyer 1990) which can lead to conflicting interpretations concerning competitive advantages (e.g. *A. triseriatus* survival is more detrimentally affected by conspecifics whereas time to eclosion is more detrimentally affected by *A. aegypti*). Because we find no clear-cut evidence that one species can maintain $\lambda' \geqslant 1·0$ while its competitor's $\lambda' < 1·0$, these species appear to be roughly equivalent competitors in this test environment without predation. We conclude that in this system, overall competitive ability is at best weakly related to behaviour, though competitive effects on some fitness components, most notably development time, may be consistent with our prediction based on behaviour.

Our finding of approximately equivalent competitive ability for these species contrasts with past competition experiments, in which investigators suggested *A. aegypti* was the superior competitor (Wilton 1968; Ho *et al.* 1989). The outcome of competition is, of course, dependent on the test environment, and there are numerous differences in experimental and analytical methods that may account for this discrepancy. First, all past studies have been done using non-natural food sources (e.g. liver powder, yeast). Our use of leaf litter as a food source creates a more realistic environment, though it would still be desirable to test competitive ability under field conditions. Secondly, all past studies focus on fitness components (e.g. survivorship, size at and time to maturity), rather than population level parameters (λ' in our case). As in our experiment, past studies have indicated an advantage for *A. aegypti* primarily in effects on development time (Wilton 1968; Ho *et al.* 1989). Because

of the problems in interpreting fitness components (see above), any single fitness component is unlikely to provide an accurate evaluation of competitive ability. In our experiment, had we only analysed time to metamorphosis, we may have concluded that *A. aegypti* had a competitive advantage over *A. triseriatus*, based on the greater impact of addition of *A. aegypti* on time to metamorphosis of both species. As indicated by other researchers (Livdahl 1984; Livdahl & Sugihara 1984; Hard, Bradshaw & Malarkey 1989; Juliano 1989; Fisher *et al.* 1990), analysis of fitness components of mosquitoes can result in misleading or contradictory conclusions.

Our results concerning the relationship of behaviour and vulnerability to predation contrast sharply with the foregoing results concerning competition. Analysis of behaviour of these two *Aedes* species results in the clear prediction that *A. aegypti* should be more vulnerable to predation. Across all stages, whether activity, position, or both are considered, this prediction is the same.

The predicted interspecific difference in short-term vulnerability to predation is strongly supported by the data from Experiment 2. Survival in the presence of *T. rutilus* declines more rapidly, and median survival times are significantly lower, for *A. aegypti* than for *A. triseriatus*. Thus, over the short term, knowing the behaviour of the two species enables us to predict survival time.

The prediction of greater long-term vulnerability to predation in *A. aegypti* is also strongly supported by our data. In Experiment 3, *A. aegypti* was virtually wiped out by predation. In contrast, although *A. triseriatus* survival at low density was reduced by predation, all cohorts exposed to predation produced at least one surviving adult. Predation appeared to increase λ' at high density, suggesting that survivors of predation benefited from reduced density due to predation, resulting in greater mass at maturity and lower time to metamorphosis, and a slight increase in λ' when exposed to predation. Thus, knowing the behaviour of the two species enabled us to predict both long-term mortality rates and estimated population growth rate when subjected to predation. Prediction of long-term vulnerability to predation based on behaviour is far more risky than is prediction of short-term vulnerability to predation. Numerous other factors could have affected mortality due to predation in Experiment 3 and rendered our prediction wrong. For example, the two species also differ in time to metamorphosis (see Figs 8 and 9), with *A. aegypti* usually reaching metamorphosis sooner (as reported by Wilton 1968; Ho *et al.* 1989). Thus, although *A. aegypti* is behaviourally more vulnerable to predation, it spends less time exposed to predation. This factor, and others, acting over the longer time scale could have obscured the greater short-term vulnerability to predation in *A. aegypti*, yet we find that knowing the behaviour of the two species enables us to predict accurately long-term vulnerability to predation.

Our prediction that the competitively superior species will also be more vulnerable to predation is also weakly supported. As noted above, if either species has a competitive advantage, it is *A. aegypti*, the species that was also more vulnerable to predation. However, any competitive advantage is not apparent at the level of population rate of change, which we consider most important for our hypothesis.

There are some striking similarities in the results of our study and those concerning relationships among behaviour, competition and predation in two congeneric damselfly larvae (Pierce *et al.* 1985; Blois-Heulin *et al.* 1990). In damselflies, the more active species was also more vulnerable to predation (Pierce *et al.* 1985; Blois-Heulin *et al.* 1990), analogous to our results for mosquitoes. In addition, the more active damselfly species was not competitively superior, and in fact appeared to be the inferior competitor (Pierce *et al.* 1985). Thus, as in our study, behavioural traits accurately predicted vulnerability to predation, but not competitive ability (Pierce *et al.* 1985; Blois-Heulin *et al.* 1990). We suspect that in most systems, even for very similar species, competitive ability will be more difficult to predict from behavioural data than will vulnerability to predation, because competitive ability is likely to be a more complex trait. Ability to harvest and deplete resources (competitive effect, Werner 1994) is only one aspect of competitive ability that must be considered along with minimum resource requirements and physiological efficiency (competitive response, Werner 1994). Only the competitive effect is likely to be simply related to activity level and foraging effort. Competition may also occur via other mechanisms (e.g. intraguild predation, other forms of interference), which are less likely to be directly related to activity level and foraging effort, further complicating prediction of competitive ability from behaviour patterns. Our results, and those for other aquatic invertebrates (Pierce *et al.* 1985; Blois-Heulin *et al.* 1990) indicate the need for further experimental tests of the generality of relationships among behaviour, vulnerability to predation and competitive ability that have been proposed based on studies with amphibians (Woodward 1982, 1983; Morin & Johnson 1988; Werner 1994).

Acknowledgements

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